Miocene sharks' teeth from Ecuador

A. E. Longbottom

Department of Palaeontology, British Museum (Natural History), Cromwell Road, London SW7 5BD

Synopsis

The first Miocene sharks from Ecuador are described. Representatives of nine genera are identified: *Procarcharodon*, *Odontaspis*, *Hemipristis*, *Galeocerdo*, *Negaprion*, *Carcharhinus*, *Scoliodon*, *Isistius* and *Aetobatus*. The shark fauna is comparable with those from the Miocene of other South American countries, the Caribbean, North America and Europe. The first occurrence of *Isistius triangulus* (Probst) in the Miocene of the western hemisphere is noted.

Introduction

During the years 1974–75, geologists from the Institute of Geological Sciences (Overseas Division) and the British Museum (Natural History) collected from the Neogene of Ecuador. Among the collections obtained were many sharks' teeth, which represent their first record from the Ecuadorian Miocene, and hence are of considerable interest. The teeth were collected by Drs C. R. Bristow and J. E. P. Whittaker. All but one of the teeth come from three localities CRB 123, a, b (Fig. 1), which occur along a 4 km stretch of coast just south of Bahia. One further tooth was collected from locality J 2a about 50 km north of Bahia. This tooth is included because of probable correlation with the beds from which the remainder were collected. The details of the localities are as follows. CRB 123 is a sea stack at Punta la Colorada, grid reference 602308, at 0° 37·6′ S, 80° 27·6′ W. CRB 123a is the cliff near the lighthouse at Punta Bellaca, grid reference 615330, at 0° 36·4′ S, 80° 27′ W. CRB 123b is the cliff at Punta la Gorda, grid reference 596298, at 0° 38·2′ S, 80° 28′ W. Grid references refer to the Cartographia Censal CC-MIII-D3 (123) Bahia de Caraquez, 1 : 50 000 map. Locality J 2a is at 0° 12′ S, 80° 20′ W.

A full description of the stratigraphy of this coastal area was published by Bristow (1976). He originally included the sharks' teeth from localities CRB 123, a, b in his faunal list for the Borbon Formation. Further work has shown, however, that the beds containing the teeth are transitional between the Onzole Formation and the overlying Borbon Formation. Here Borbon-type sandstones sometimes occur in Onzole-type blue silts and *vice versa* and it is difficult to refer the teeth to either of these Formations with certainty. Planktonic foraminifera from nearby sample CRB 124 (grid reference 609318) have dated these transitional beds as Zone N17 of Blow (1969), late Miocene (J. E. P. Whittaker, personal communication). Age-diagnostic species are *Sphaeroidinellopsis paenedehiscens* Blow, *Globorotalia plesiotumida* Blow & Banner and *Globorotalia humerosa* Takayanagi & Saito. The sample J 2a is from a part of the so-called Jama Formation which is thought to be equivalent to the Borbon Formation and also late Miocene.

The matrix is a medium-grained sandstone which has been recemented by weathering, especially at locality CRB 123, the sea stack from which the teeth were partly eroded out. This means that it is extremely hard and is difficult to remove without breaking the specimens. It tends to adhere more strongly to the roots, thus allowing only the crowns to become visible. Consequently many specimens consist of crown only.

The teeth described are all now deposited in the collections of the British Museum (Natural History), London, and are referred to in this paper by the register number of that institution with a 'P' prefix.

Faunal Description

The fauna includes 9 genera, with 10 species, all in the subclass Selachii. Measurements quoted are the vertical height of the complete tooth, unless otherwise stated.

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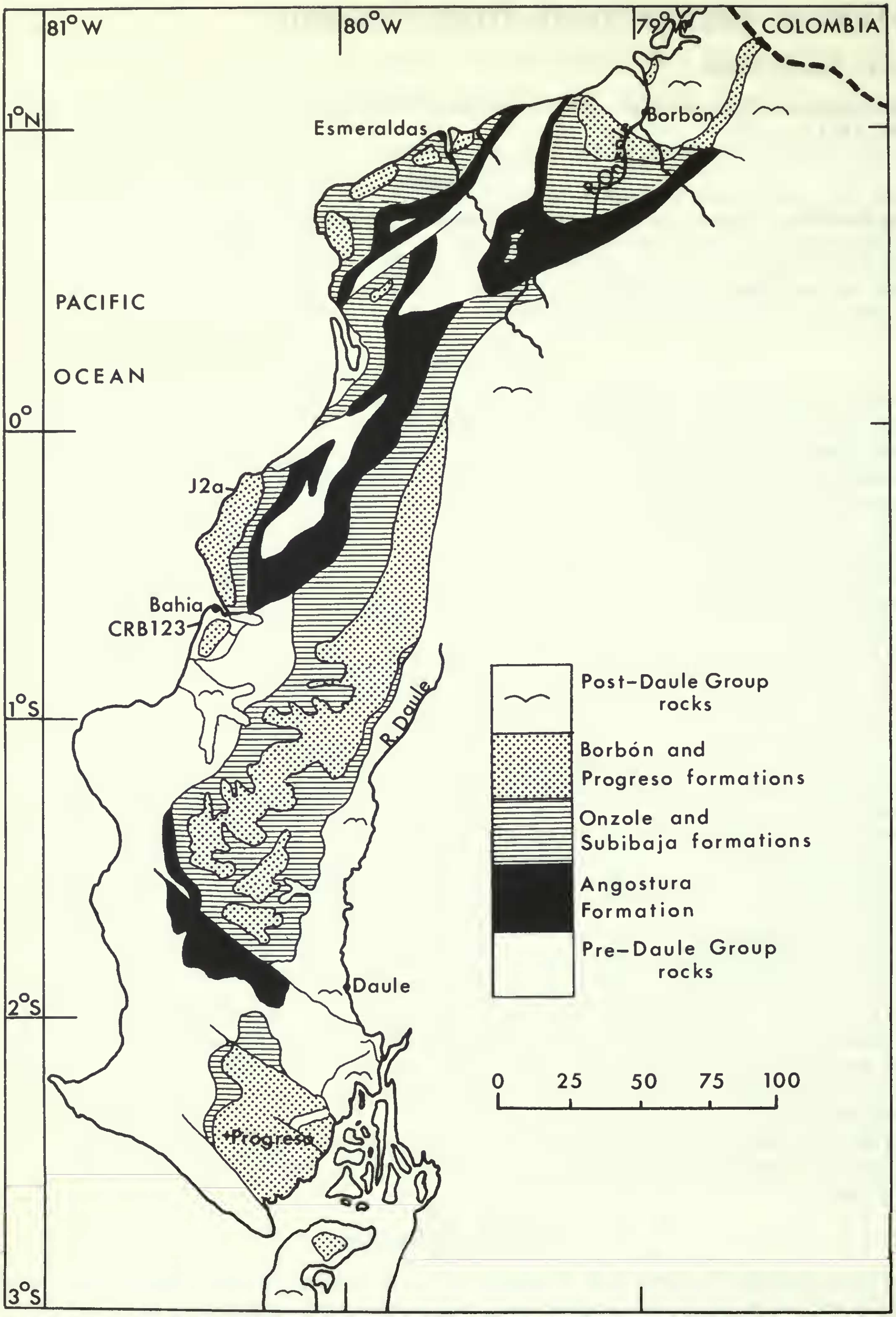


Fig. 1. Generalized geological and locality map of part of coastal Ecuador (from Bristow 1976); CRB 123 and J 2a are C. R. Bristow sample locality numbers.

Class **CHONDRICHTHYES**

Subclass **SELACHII**

Family **ISURIDAE**

Genus ***PROCARCHARODON*** Casier
Procarcharodon megalodon (Agassiz)

SYNONYMY. See Cappetta (1970).

MATERIAL. Four incomplete specimens, P.59278–81.

LOCALITIES. Three from CRB 123, one from CRB 123b.

DESCRIPTION (Fig. 2). The teeth are all fairly large (estimated height 8–9 cm) and typical of this species.

Family **ODONTASPIDAE**

Genus ***ODONTASPIS*** Agassiz
Odontaspis acutissima Agassiz

SYNONYMY. See Cappetta (1970).

MATERIAL. Eleven teeth, P.59265–74.

LOCALITIES. Nine from CRB 123, two from CRB 123b.

DESCRIPTION (Figs 3, 4). The teeth are typical of this species. Most of them lack a root and denticles, but they all have vertical striations on the inner face of the crown. Most appear to be anterior teeth.

Family **CARCHARHINIDAE**

Genus ***HEMIPRISTIS*** Agassiz
Hemipristis serra Agassiz

SYNONYMY. See Cappetta (1970).

MATERIAL. Two specimens, P.59275–6.

LOCALITY. Both from CRB 123.

DESCRIPTION. One specimen consists of the root only and the other is the apex of a crown.

Genus ***GALEOCERDO*** Müller & Henle
Galeocerdo aduncus Agassiz

SYNONYMY. See Cappetta (1970).

MATERIAL. One tooth, P.59277.

LOCALITY. CRB 123.

DESCRIPTION. This specimen is an almost complete tooth, still partly embedded in the matrix. The tooth is large, being 2·3 cm across the widest part at the base of the crown. The tip of the crown is missing so the height cannot be measured.

Genus *NEGAPRION* Whitley

Isolated teeth of this genus are difficult to distinguish from the lower teeth of some species of *Carcharhinus*. From descriptions of fossil and Recent (Bigelow & Schroeder 1948) examples of this genus some of the specimens in this collection are included in the genus *Negaprion*. All the specimens are here identified as *N. eurybathrodon* (Blake).

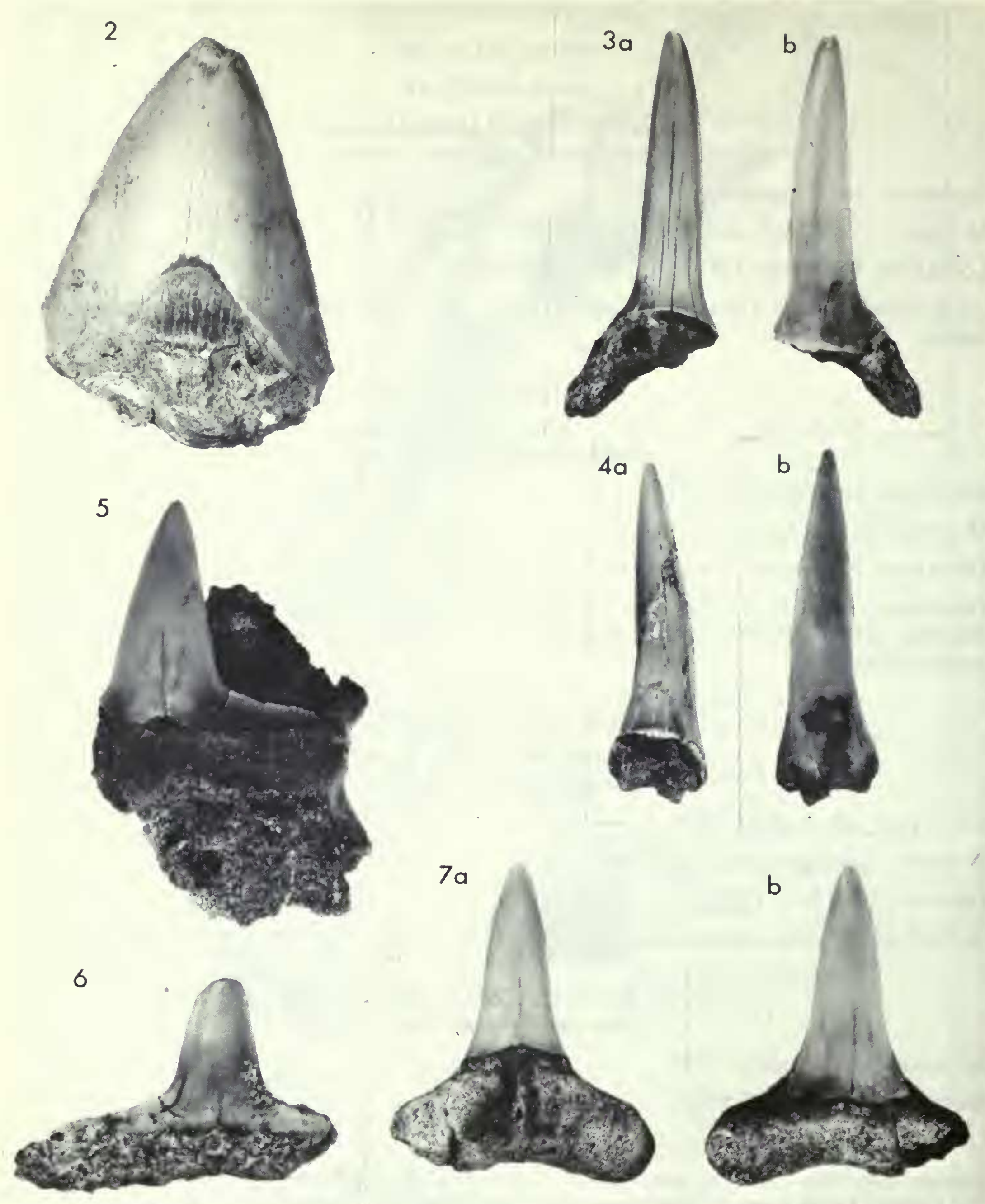


Fig. 2. *Procarcharodon megalodon.* P.59280, CRB 123, inner view, ×0·7.
Figs 3–4. *Odontaspis acutissima*, both CRB 123. (3) P.59267. (4) P.59266. (a) inner views; (b) outer views. ×2.
Figs 5–7. *Negaprion eurybathrodon.* (5) P.59262, CRB 123, outer view, ×2·2. (6) P.59263, CRB 123a, outer view, ×2·9. (7) P.59257, CRB 123 : (a) inner view; (b) outer view; ×2·4.

Negaprion eurybathrodon (Blake)

SYNONYMY. See Cappetta (1970).

MATERIAL. Nine teeth, P.59257–64.

LOCALITIES. One from CRB 123a, seven from CRB 123, one from CRB 123b.

DESCRIPTION (Figs 5–7). Some of the teeth are fairly complete, others incomplete or still partly embedded in matrix. Two of the larger teeth (heights 1·7 and 2 cm) appear to be upper teeth by White's (1955) description. These have more triangular crowns than the lower teeth, and flatter outer faces. They have a small central depression in the base of the enamel of the outer face. The lateral extensions of enamel along the roots have wavy edges. These two teeth are slightly asymmetrical and are probably lateral in position, since they also have wide roots.

The lower teeth are symmetrical, even those most lateral ones with wide roots. The lateral extensions of the enamel, when visible, show only slight crinkling along the edges in some specimens. The teeth have a convex inner face and a bulbous outer face to the crown, especially at the base of the enamel. It is this character, and the lack of serrations on the main part of the crown, that distinguishes these teeth from the lower teeth of the *Carcharhinus* species in this fauna.

Genus *CARCHARHINUS* Blainville

This genus contains many living species with a variety of tooth types. The upper teeth tend to have triangular crowns with fine regular serrations along the edges. The lower teeth have narrower upright crowns with or without serrations, depending on the species. The unserrated lower teeth of some species are difficult to distinguish from those of species in other genera (e.g. *Negaprion*, *Hypoprion*) and other anatomical details are used in identifying Recent species, since teeth alone are not reliable. Fossil teeth of the unserrated type can therefore only be arbitrarily attributed to a genus and species, as with the foregoing *Negaprion*. The same is true when trying to associate upper and lower teeth as one species. I have placed two of the following types of teeth into one species, *C. egertoni*, because of custom, and because they fit the accepted descriptions of this species in Leriche (1942).

Carcharhinus egertoni (Agassiz)

SYNONYMY. See Antunes & Jonet (1969).

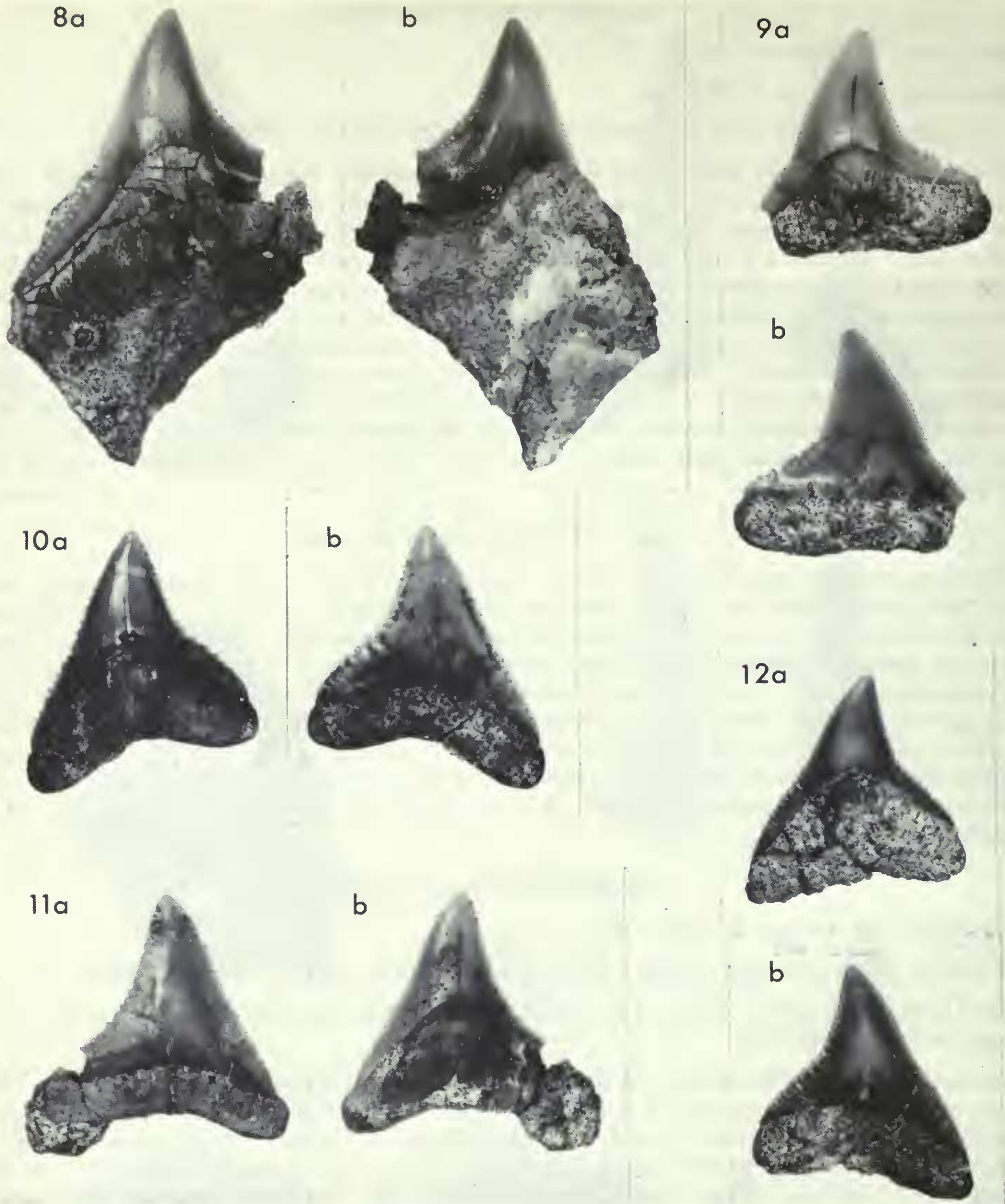
MATERIAL. Forty-nine upper teeth, P.59215–236, P.59244–6. Six lower teeth, P.59237–42.

LOCALITIES. Upper teeth, 43 from CRB 123, two from CRB 123a, four from CRB 123b. Lower teeth, six from CRB 123b.

DESCRIPTION (Figs 8–19). Most of the upper teeth lack roots or are embedded in the matrix. They have broadly triangular crowns on a wide root. The crowns all show strong regular serrations, which become slightly coarser towards the base. The heights of the crowns vary from 7·3 mm to 15 mm, and within the sample there is a continuous size range. Anterior and lateral teeth are present, with the crowns becoming more asymmetrical and the roots becoming wider in the lateral teeth. There are crenulations at the base of the enamel on the outer face of the larger teeth. Many teeth have a central, raised pad of enamel at the base of the outer face.

In these teeth the roots are narrower and the serrations finer than those of *Carcharhinus priscus*. The crowns also tend to be more triangular. The central pad of enamel is not present in *C. priscus*. The majority of the teeth are larger than described examples of *C. priscus*.

The lower teeth are much fewer and are restricted to one locality. They have slender crowns which are symmetrical. All the specimens collected have narrow roots. The outer faces are more convex than those of the upper teeth. The crowns bear serrations at the tip only and when viewed from the outer side the crowns expand at the serrated part. In most the cutting edge is only strongly developed at the tip and is not very clear on the lower half of the crown. This is not due to wear since the fine serrations are still visible at the tip.

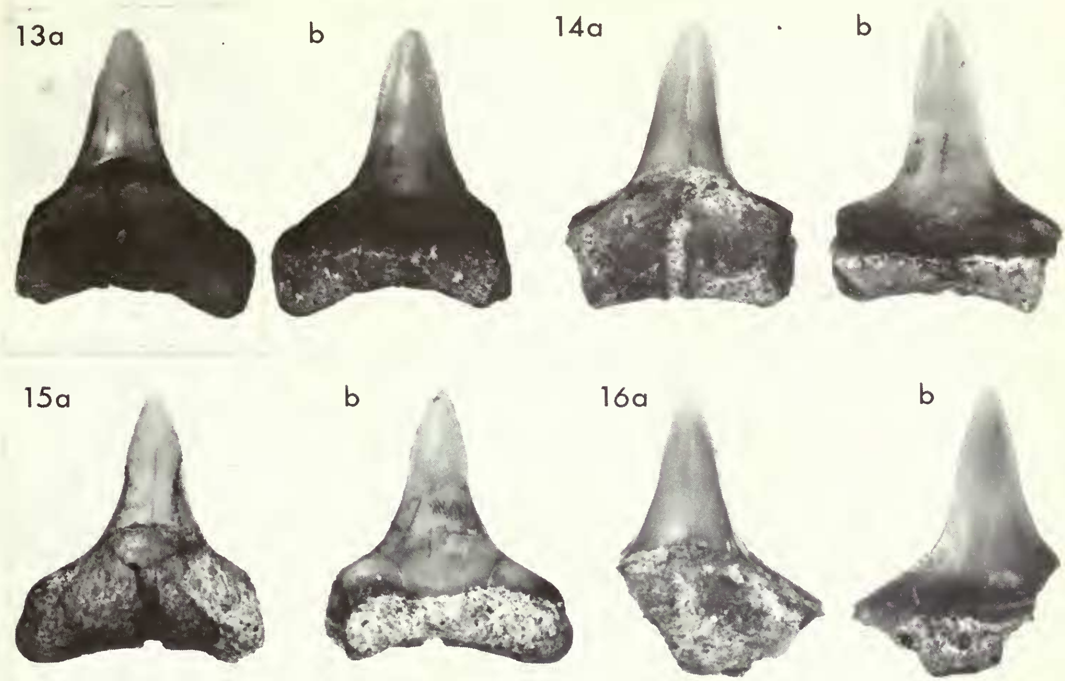


Figs 8–12. *Carcharhinus egertoni*, upper teeth, all CRB 123. (8) P.59215. (9) P.59225. (10) P.59217. (11) P.59216. (12) P.59219. (a) inner views; (b) outer views. All approx. ×2.

These teeth fit the description of *C. egertoni* by Leriche (1942 : fig. 6). As White (1955) says, there does not seem to be much difference between this species and the Recent *Carcharhinus longimanus* (Poey), the lower teeth being very similar.

The difference in the numbers of upper and lower teeth may be an effect of preservation or collection. However, there is a possibility that the upper teeth represent more than one species. Two of the smaller ones show some similarity to *C. priscus* in having narrower crowns and coarser serrations.

Three of the upper teeth (Figs 17–19) show some variation. The crowns lean distally. The distal edge is concave and the mesial edge convex, especially so about half-way up the crown. This pronounced convexity is not present in the other specimens. Leriche (1942 : pl. 8, fig. 4) and Eastman (1904 : fig. 1) figure teeth similar to these as *C. egertoni*.



Figs 13–16. *Carcharhinus egertoni*, lower teeth, all CRB 123b. (13) P.59237, ×3. (14) P.59238, ×3. (15) P.59239, ×2·5. (16) P.59240, ×3. (a) inner views; (b) outer views.

Carcharhinus cf. ***priscus*** (Agassiz)

SYNONYMY. See Cappetta (1970).

MATERIAL. Seven ? lower teeth, P.59247–53.

LOCALITIES. Six from CRB 123, one from CRB 123b.

DESCRIPTION (Figs 23–24). The teeth all have slender crowns on wide bases. The crowns are upright or incline slightly distally. These teeth also have fine serrations along the whole edge of the crown. They are very similar to the following species but are much smaller.

These teeth are like those of *C. priscus* shown in Cappetta (1970 : pl. 14, figs 1–20) and examples in the British Museum (Natural History) from Montpellier and Florida. However, they have more definite serrations and the roots are separated by a more acute angle. The crowns are also narrower.

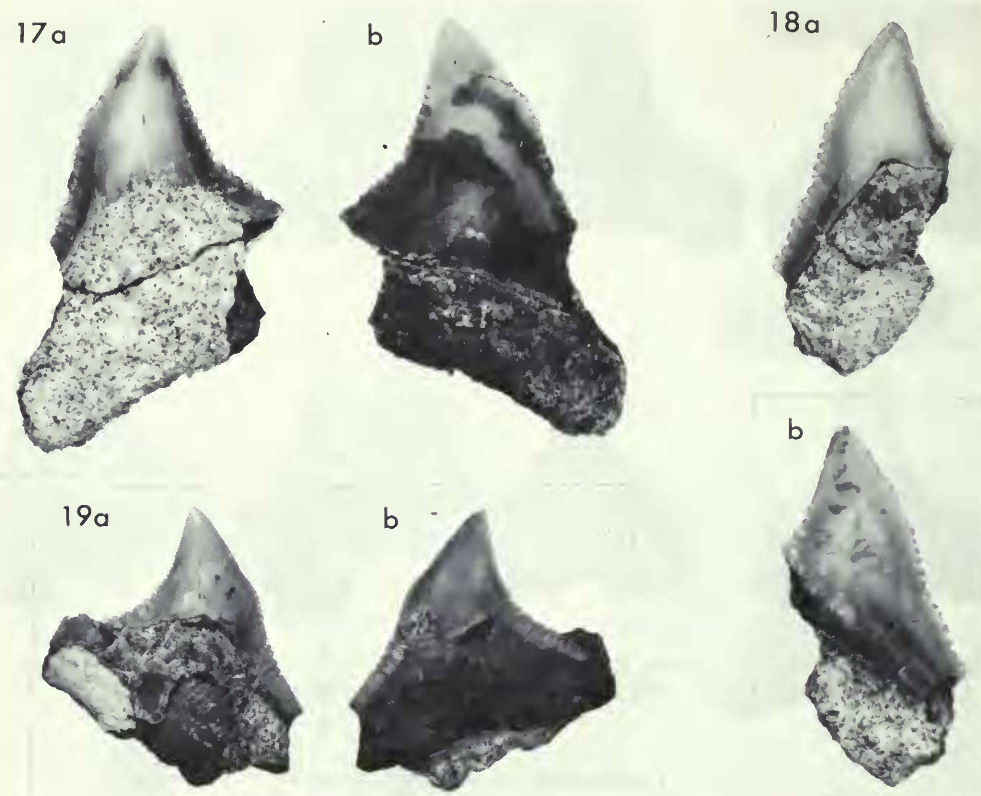
Carcharhinus sp.

MATERIAL. Three ? lower teeth, P.59254–6.

LOCALITIES. Two from CRB 123, one from J 2a.

DESCRIPTION (Figs 20–22). The teeth have symmetrical crowns on wide bases. The crowns are narrower than those of the upper teeth of *C. egertoni*. The outer face is slightly convex, the inner more so. These teeth have fine regular serrations along the whole edge of the crown and along the basal lateral extensions of enamel, and so differ from the lower teeth of *C. egcrtoni*. The teeth are fairly large and measure 1·6 cm, 1·49 cm and 1·35 cm in height.

The teeth are similar to upper teeth of *C. priscus*, but differ in their larger size and finer crenulations. These crenulations do not become coarser towards the base as they do in *C. priscus* and *C. egertoni*.



Figs 17–19. *Carcharhinus egertoni*, upper teeth, all CRB 123. (17) **P.59244**, ×2·9. (18) **P.59245**, ×2·6. (19) **P.59246**, ×1·8. (a) inner views; (b) outer views.

Genus ***SCOLIODON*** Müller & Henle

Scoliodon taxandriae Leriche

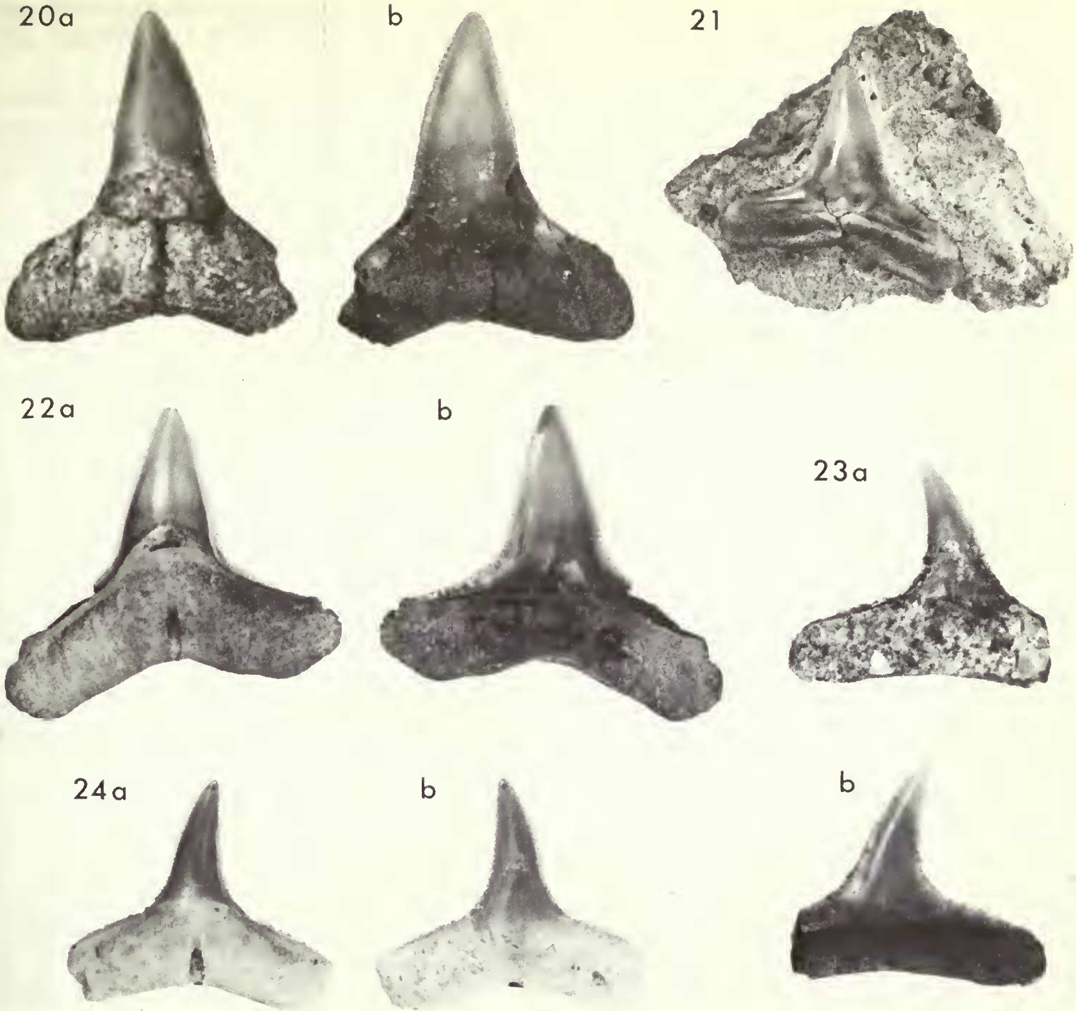
SYNONYMY. See Antunes & Jonet (1969).

MATERIAL. Four teeth, P.59285–8.

LOCALITY. CRB 123b.

DESCRIPTION. Two of the teeth (P.59285–6) have triangular crowns which are inclined distally. The mesial edge is a continuous concavity, the distal edge is more or less vertical and has a notch where it joins the distal denticle. The distal denticle has a slightly wavy edge. The inner and outer faces are convex, with the enamel on the outer face ending basally in a horizontal pad. A distinctive oblique nutritive groove on the inner face also produces a notch visible, from the outer side, between the roots.

The two other teeth are about the same size as the previous two (5·5 mm and 3·7 mm high). They are similar to the above teeth except that the mesial edge is less concave and the outer



Figs 20–22. *Carcharhinus* sp. (20) P.59254, CRB 123; (a) inner view; (b) outer view; ×2·9. (21) P.59255, CRB 123, outer view; ×2. (22) P.59256, J 2a, (a) inner view; (b) outer view; ×2·3.
Figs 23–24. *Carcharhinus priscus*. (23) P.59247, CRB 123, ×3·8. (24) P.59253, CRB 123b, ×3·5. (a) inner views; (b) outer views.

face is flat. Instead of a horizontal pad at the base of the outer face, there is a medial triangular depression in the enamel.

Family SCYMNORHINIDAE

Genus *ISISTIUS* Gill
Isistius triangulus (Probst)

Synonymy. See Cappetta (1970).

Material. Three lower teeth, P.59282–4.

Localities. Two from CRB 123, one from CRB 123a.

Description (Figs 25–26). Two of the specimens are still partly embedded in matrix. One of these shows half the root with an indication of the central foramen (Fig. 25). The other two specimens are crowns only. One specimen shows an indication of crenulations along the edge. All three crowns are triangular, very thin and typical of this species. They are all anterior teeth and fairly large for this species, with crown heights of 4·5 mm.

This is the first definite record of *Isistus triangulus* in the Miocene of the western hemisphere. Casier (1958) described specimens of *Isistius* sp. from Barbados. In 1966 he redescribed them as *Sphyraena kugleri* Casier and figured more examples. However, his pl. 3, fig. 27 appears to be a specimen of *Isistius triangulus* and is thus included in Table 1.

Family MYLIOBATIDAE

A few teeth of *Aetobatus* sp. and possibly *Myliobatis* sp. are present in the fauna but these are very worn or still embedded in the matrix and are not identifiable to species.

Figs 25–26. *Isistius triangulus*, lower teeth. (25) P.59284, CRB 123a, inner view. (26) P.59282, CRB 123, outer view. Both ×6·6.

Discussion

This is the first fauna of sharks to be described from the Miocene of Ecuador. The Miocene deposits along the coast of Ecuador are up to 5000 ft (1520 m) thick (Sheppard 1928) and much work has been done on the foraminifera and mollusca of these deposits. References to Miocene sharks from South America are sparse. Table 1 is a summary of the known geographical distribution of the species in this fauna. I know of no references to sharks' teeth from the Miocene of Colombia. Small faunas from Chile (Oliver-Schneider 1936, 1937), Peru (Hoffstetter 1968) and Venezuela (Leriche 1938, Rodríguez 1968) contain little more than the cosmopolitan *Procarcharodon megalodon*. The Peruvian fauna is thought to be uppermost Miocene like the one from Ecuador. Leriche (1938) says that *Hemipristis serra* and *P. megalodon* from Venezuela are also from the Upper Miocene. The other faunas are merely stated as being from the Miocene.

Of the other South American countries, a large fauna is described from the Pirabas Formation of Brazil (Santos & Travassos 1960, Santos & Salgado 1971). This fauna is Lower Miocene in age, older than the Ecuador fauna, but five species are common to both faunas. The Brazilian fauna includes *Scoliodon taxandriae*, and this is the only other record of this species from the western hemisphere.

Records of the Argentinian Miocene faunas are controversial. Sharks' teeth from the Patagonian and Paraná formations have been described. Leriche (1907) described sharks from the

Table 1. The geographical distribution of the species

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
Procarcharodon megalodon	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Odontaspis acutissima	+			+				+	+				+			+		ø[1]					+	+	+	+	+	+	+	+	+	+	+	+
Hemipristis serra	+			+	+	+	+	+	+			+	+	+	+	+	+	+	+	+	+		+	+	+	+	+	+	+	+		+	+	+
Galeocerdo aduncus	+			+					+				+		+	+	+	+	+	+	+		+	+	+	+	+	+	+	+	+	+	+	+
Negaprion eurybathrodon	+													+		+	+			+						+								+
Carcharhinus egertoni	+		+	+		+	+	+								+	+	+	+	+						+							+	
Carcharhinus priscus	+		+	+		+									ø	+					ø		+	+	+	+	+	+	+	+	+	+	+	
Carcharhinus sp.	+																																	
Scoliodon taxandriae	+					+																	+			+					+			
Isistius triangulus	+							+															+			+		+		+				
Aetobatus arcuatus[2]					+										ø	+	+		+		ø		+	+	+	+		+	+	+		+		

South America

1 Ecuador
2 Chile (Oliver-Schneider 1936)
3 Peru (Hoffstetter 1968)
4 Argentina (Leriche 1907, Woodward 1900, Ameghino 1906, Pascual & Rivas 1971)
5 Venezuela (Leriche 1938, Rodríguez 1968)
6 Brazil (Santos & Travassos 1960, Santos & Salgado 1971)

Caribbean

7 Trinidad (Leriche 1938, Casier 1958)
8 Barbados (Leriche 1938, Casier 1958, 1966)
9 Cuba (Leriche 1938, Kruckow 1957)
10 Jamaica (Leriche 1938)
11 Haiti (Leriche 1938)
12 Mexico (Leriche 1938, Kruckow 1959)
13 Baja California (Kruckow 1957)
14 Panama (Leriche 1938, White 1955)

North America

15 California (Leriche 1942)
16 Maryland (Leriche 1942, Eastman 1904)
17 North Carolina (Leriche 1942)
18 South Carolina (Leriche 1942)
19 Virginia (Leriche 1942)
20 New Jersey (Leriche 1942)
21 Florida (Leriche 1942)
22 Mississippi (Leriche 1942)

Europe

23 Montpellier (Cappetta 1970)
24 East France (Cappetta 1970)
25 Italy (Cappetta 1970)
26 Portugal (Cappetta 1970, Antunes & Jonet 1969)
27 Spain (Cappetta 1970)
28 Switzerland (Cappetta 1970, Leriche 1927)
29 Austria (Cappetta 1970)
30 Germany (Cappetta 1970)
31 Belgium (Cappetta 1970)
32 Holland (Cappetta 1970)

33 *Africa* (Cappetta 1970, Dartevelle & Casier 1943)

34 *Australia* (Cappetta 1970, White 1955)

[1] ø indicates specimens from this locality present in the British Museum (Natural History) collections, but not mentioned in the references.
[2] This species is included for comparison, since the *Aetobatus* specimens from Ecuador are not identified to species.

Patagonian and thought it might contain a mixture of Miocene (with *Isurus hastalis* (Agassiz), *Procarcharodon megalodon* and *Galeocerdo aduncus*) and Oligocene species (with *Odontaspis cuspidata* Agassiz and *Isurus desori* (Agassiz)). Priem (1911) thought the fish and cetaceans indicated an Early Miocene age for the Patagonian, whereas the molluscs indicated an Eocene/Cretaceous age. Ameghino (1889, 1906) described the Tertiaries of Argentina in great detail. He gave a list of sharks found in the Patagonian and said it was probably Early Eocene in age, despite the presence of Cretaceous species such as *Corax rothi* Ameghino, *Isurus angustidens* (Reuss) and *Scapanorhynchus subulatus* (Agassiz).

Ameghino also gave a faunal list for the Paraná group. This includes *Carcharhinus egertoni*, *Procarcharodon megalodon*, *Galeocerdo aduncus* and other typical Miocene species. He said they came from the marine Enterienne Formation of Paraná, and concluded the formation was Upper Oligocene in age. Woodward (1900) questioned this and because of the presence of the above sharks thought the Paraná was Upper Miocene or Lower Pliocene. More recently Pascual & Rivas (1971) have revised the vertebrate faunas of the Tertiary of Argentina. They give a shark faunal list, based on the works of Ameghino, for the marine facies of the Patagonian Formation and the 'Enterriense'. They arrive at a Lower Miocene age for the Patagonian, based on the cetacean and penguin faunas also found. Simpson (1972 : 6) agrees with this and says: 'Some marine beds confused with or even included in parts of the Patagonian Formation may be older, but it remains highly probable that the greater or typical part of the formation is not older than late Oligocene, more likely early Miocene, and that the same determination applies to the fossil penguins.' The shark fauna, as stated earlier, includes many Eocene and Cretaceous species.

Pascual & Rivas (1971) give faunal lists for the 'Enterriense', 'Mesopotamiense' and 'Rionegrense' of the Paraná. The shark determinations again are probably from Ameghino and include usual Miocene forms. The majority of other vertebrates listed, however, are terrestrial mammals and these indicate a Pliocene age for the Paraná. Pascual & Rivas say that there seems to be a mixture of terrestrial and marine faunas and they have included all the genera cited in previous works whether terrestrial or marine. They say that the rarer forms seem to be older and possibly represent secondarily derived fossils. They do not say whether they consider the sharks to be derived. This does seem possible in view of their probable Miocene age.

I have included *P. megalodon*, *O. acutissima*, *C. egertoni*, *C. priscus*, *H. serra* and *G. aduncus* in Table 1 as being probably from the Miocene of Argentina based on the above evidence.

The information for the Caribbean region is mostly from Leriche (1938); other references are given in Table 1. Most of the faunas are merely described as Miocene in age. Exceptions to this are the specimens of *N. eurybathrodon* from Panama, which are from the Middle Miocene (White 1955). Casier (1958) describes *H. serra*, *P. megalodon* and *C. egertoni* from the Lower Miocene of Trinidad, and *C. egertoni* and *H. serra* from the Upper Miocene. The Bissex Hill Formation of Barbados is Lower Miocene and considered to be contemporaneous with the Calvert Formation of Maryland (Casier 1958, 1966). *P. megalodon* and *H. serra* from Mexico are also from the Lower Miocene (Leriche 1938, Kruckow 1959).

The information for the North American faunas is taken from Leriche (1942) and Eastman (1904). The Maryland faunas have been studied by Eastman (1904), however the sharks' teeth all come from the Calvert Formation in the Lower Miocene. *Aetobatus arcuatus* is the only species recorded from the St Mary's Formation (Upper Miocene) by Eastman. Leriche (1942) says that a specimen of *Odontaspis acutissima* is also possibly from the Upper Miocene. The other American records in Leriche (1942) are Lower Miocene or undifferentiated Miocene. There are many more recent references to the Miocene of North America but it is not within the scope of this paper to review them all.

The European distributions are taken from Cappetta (1970) and Antunes & Jonet (1969). Cappetta gives a good comparison of these faunas, including Lower, Middle and Upper Miocene. Table 2 (taken from Cappetta (1970) and Antunes & Jonet (1969)) shows that all the Ecuadorian species range into the Upper Miocene in Europe. The faunas from Montpellier and Portugal correspond closely to that of Ecuador. The Montpellier fauna does not include *C. egertoni*, *N. eurybathrodon* and the *Carcharhinus* sp., but the first two are present in Portugal.

The Ecuadorian fauna is therefore typically Miocene and compares closely with those of

Table 2. Distribution of the species in the Oligocene and Miocene

	Olig. L	Olig. M	Olig. U	Mioc. L	Mioc. M	Mioc. U
Procarcharodon megalodon				I	—	I
Odontaspis acutissima	I	—	—	—	—	I
Hemipristis serra				I	—	I
Galeocerdo aduncus			I	—	—	I
Negaprion eurybathrodon				I	—	I
Carcharhinus egertoni				I	—	I
Carcharhinus priscus		I	—	—	—	I
Scoliodon taxandriae				I	—	I
Isistius triangulus					I	I
Aetobatus arcuatus				I	—	I

Montpellier and Portugal, both of which have been very well studied. It differs from the Montpellier fauna in the absence of small sharks' teeth of several species. Further collecting in Ecuador is necessary for the study of the shark-tooth microfauna.

Table 3 shows the bathymetric and climatic ranges of Recent members of the genera present in the Ecuador collection. The molluscan and foraminiferal faunas of the Miocene of Ecuador both indicate deposition in warm, fairly shallow water. This interpretation is supported by the shark fauna, which has a predominance of supposed near-shore littoral forms. The Recent species are also tropical to subtropical in range. *Isistius* is the only pelagic form, but this is also neritic in habit, and could range into shallower water.

This fauna from Ecuador is important for the confirmation of the presence of *Scoliodon taxandriae* and *Isistius triangulus* in the western hemisphere, and in the variety of *Carcharhinus* teeth present. Future collections from the Miocene deposits of Ecuador, and also Colombia, could prove useful in furthering the study of the genus *Carcharhinus* and in extending the known geographical range of other Miocene species.

Table 3. Bathymetric and climatic ranges of the genera

	littoral	pelag.	bathy.	trop.	sub-trop.	temp.
Carcharodon	=	+		=	+	
Odontaspis	×	=		=	+	=
Hemipristis	+			×	=	
Galeocerdo	+	+		+	×	=
Negaprion	×			×	=	
Carcharhinus	=	+		+	+	
Scoliodon	×	=		+	+	
Isistius		×	=	+	+	
Aetobatus	+			+		

× occurrence abundant + occurrence common = occurrence rare

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